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ON THE DYNAMICS OF VARIOUS RHYTHMS IN THE ELECTROCORTICOGRAM OF A CAT ASLEEP AND AWAKE

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ABSTRACT. The dynamics of cortico- and subcorticograms of cats was studied at different phases of sleep and wakefulness by means of spectral analysis and the integration method. The data obtained on 16 animals a) in drowsy state; b) during presentation of a conditioned signal; and c) during the stimulation of the reticular formation were statistically processed.

The threshold stimulation of the reticular formation (RF) in slow sleep depressed the slow rhythms (delta and alpha), as well as beta-1 waves in the auditory and visual cortex. The beta-2 rhythms did not undergo any changes.

Supraliminal RF stimulation produced a more general depression of all cortical rhythms and simultaneously a behavioral arousal. Spontaneous arousal or that evoked by a conditioned signal was attended with the same EEF changes.

In the hippocampus, as the stimulation increased, a general depression of all rhythms ("desynchronization") set in gradually, as well as delta- and theta waves dominance. This indicates involvement of hypothalamic connections in local electrogenesis.

The above data suggest the need of revising the generally accepted definition of "desynchronization", based on a visual analysis of EEG records when fast rhythms are masked during synchronized sleep periods.

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It is well known that the transition from a state of sleep to that of wakefulness is accompanied by abrupt changes in the character of the electroencephalogram (Moruzzi and Magoun [12], Bremer [5]), expressed by a depression or desynchronization of the slow and comparatively high-amplitude electric fluctuations which are characteristic of the sleep state. It is also firmly established that during awakening, at the same time that slow waves are depressed, there is an intensification and increase in frequency of the comparatively rapid and low-amplitude electric fluctuations (Moruzzi and Magoun [12], Bremer [5], Jasper et al. [9], Jouvet [10], Gastaut [7], Walter and Adey [16], Routtenberg [13], Grossman [8]). In the literature available to us, works are also encountered which show that in the desynchronization of slow electric activity, it is also possible that no increase occurs in comparative rapid and low-amplitude fluctuations (Rusinov [3], Grindel' et al. [2], Yokota and Fujimori [14]). But these works evidently have had no significant effect on the generally-accepted hypothesis, which was formulated on the basis of a study of the dynamics of the total electroencephalogram. For the systematic study of this question, we used the method of spectral analysis and integration of the electroencephalogram which makes possible a quantitative calculation of changes in various rhythms in the total electric activity during various states of the animal.

Method

Tests were made on cats. Factory-insulated metal electrodes, 150 - 200 μ in diameter, were chronically introduced into various areas of the neocortex and in the mesencephalic reticular formation. The electrocorticogram recording was made on a 13-channel ink-writing electroencephalograph made by the "Sanei" company. A 2-channel analyzer-integrator made by the same company was used to make a spectral analysis of the electric activity of the visual, auditory, sensory-motor and the two associative areas of the neocortex.

Integrated values of individual rhythms were quantitatively analyzed, and the reliability of the resulting changes was determined by the Student T-criterion (Winer [17]).

Stimulation was produced by square pulses from a high-frequency generator. Conditioned sound signals were also used as stimuli.

After the tests ended, the cats were killed, the brain fixed in 10% Formalin, and the site of electrode endings determined in serial sections.

Results of the Research and Their Discussion /129

Figure 1 illustrates the electric activity of the auditory and visual sections of the neocortex and the dorsal hippocampus of a sleeping cat and its change under the influence of electric stimulation of the mesencephalic reticular formation. Before stimulation begins, slow high-amplitude fluctuations predominate in all structures (Figure 1 A). The values of individual rhythms, integrated for a 10-second period, show that during sleep δ, θ and α-rhythms predominate both in the auditory area of the neocortex and in the hippocampus. In response to liminal stimulation of the reticular formation (Figure 1 A), especially abrupt changes appear in the electric activity of the neocortex and are expressed by strong depression of δ, θ and α-rhythms. β_1-rhythm is also significantly depressed, but β_2 does not undergo any changes. In the hippocampus, δ and α-rhythms are decreased, but to a much lesser degree than in the neocortex. Still more weakly depressed is the θ-rhythm of the hippocampus.

With stronger stimulation of the reticular formation, behavioral awakening ensues, changing to alertness of the animal (Figure 1 B). At this time, a depression of δ, θ and α-rhythms is observed in the neocortex. β_1-rhythm is also depressed, but β_2 does not undergo significant changes. The electric activity of the hippocampus changes much more significantly — δ-rhythm is depressed, and θ-rhythm is intensified. β_1 and β_2 rhythms of the hippocampus do not change markedly.

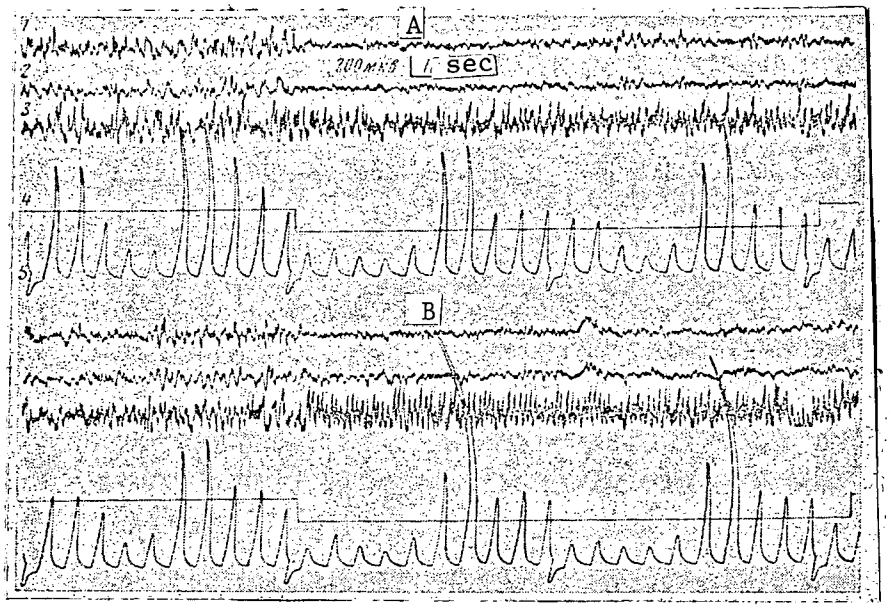

Figure 1. Change in electric activity in the auditory section of the neocortex (1), visual section (2) and the dorsal hippocampus (3) under the effect of: A - liminal (1.5 V, 100 per second, 0.1 msec) and B - supra-liminal (3 V, 100 per second, 0.1 msec) stimulation of the mesencephalic reticular formation. 4 - stimulation marking; 5 - integrated rhythm values: 2-4 cps (δ), 4-8 cps (δ), 8-13 cps (α), 13-20 cps (β_1) and 20-3 cps (β_2) of the auditory cortex (first five deflections) and the dorsal hippocampus (next five deflections).

It is clearly evident from the pattern described above that comparatively high-frequency and low-amplitude (β_1 and β_2) rhythms do not increase in frequency or intensify in the auditory section of the neocortex during awakening. Neither do they intensify when an emotional reaction of alertness and alarm develops in the animal. A thorough study of many specimens has shown that a /130 similar pattern is also observed in other areas of the neocortex. Figure 2 illustrates the change in the electric activity of four neocortical areas under various influences. In drowsiness, typical spindle-shaped potentials develop in the sensory-motor cortex (Figure 2, A, 1); in the auditory cortex

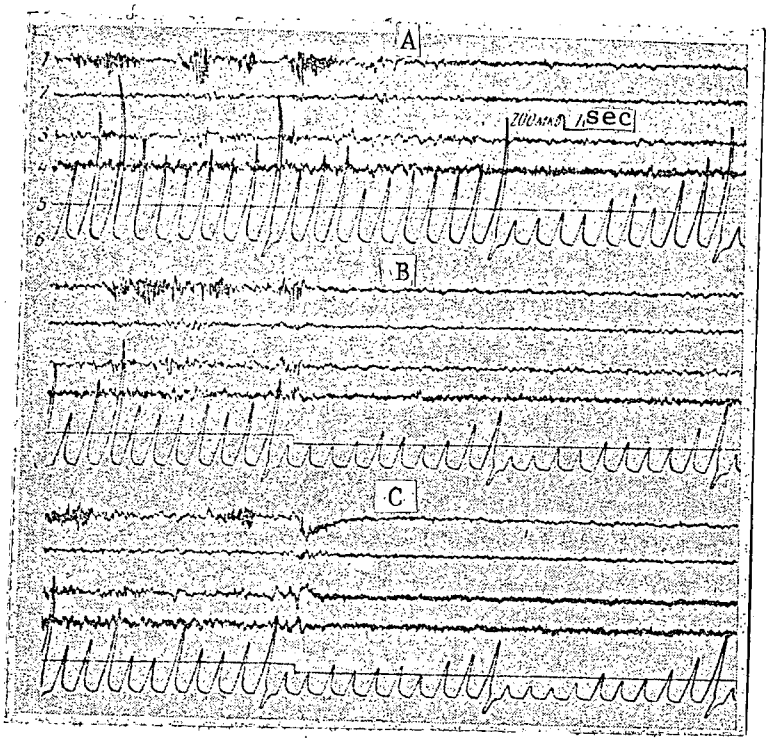

Figure 2. Change in electric activity in the sensory-motor (1), visual (2), associative (3) and auditory (4) sections of the neocortex in spontaneous awakening (A), in awakening in response to a sound stimulus (B) and in response to stimulation (C) of the reticular structure (3 V, 100 per second, 0.1 msec). 5 - stimulation marking; 6 - integrated rhythm values: δ, θ, α, β_1 and β_2 of the sensory-motor (first five deflections) and the auditory (next five deflections) regions.

the predominance of β_2 rhythm (20-30 cps) attracts attention. This is rarely observed in neocortical structures. When the animal awakens spontaneously, desynchronization appears in the recorded structures of the neocortex, expressed by a depression of all rhythms, especially in the sensory-motor cortex. Simultaneously with the depression in the amplitude of δ, θ and α-rhythms, β_1 and

β_2-rhythms are also significantly depressed. A depression of β-rhythms, although to a lesser degree, is also noted in the auditory cortex.

In response to a conditioned sound signal (Figure 2, B) and electric stimulation of the reticular formation (Figure 2, C), not only the slower rhythms (δ, θ and α) are depressed, but β-rhythms as well, although the degree of depression of the latter is less in the auditory cortex than in the sensory-motor cortex.

In cases of pronounced β-rhythms in the auditory area of the neocortex, their dynamics attract attention at various depths of slow sleep. It was shown that during deep, slow sleep, β_2-rhythm in the auditory cortex of these cats is significantly depressed (Figure 3, B — beginning of the tracing) in comparison with a state of drowsiness (Figure 3, A). If a conditioned sound signal is given against this background, when the animal awakens, at the same time that all other rhythms of the auditory cortex are depressed, β_2-rhythm is not only not depressed, but is significantly intensified (Figure 3, B). However, its amplitude after the conditioned signal is terminated and the drowsy state restored is not decreased, but even increases (Figure 3, C). This indicates that this rhythm is depressed only during deep, slow sleep.

With the exception of this case, we noted no intensification and increase in frequency of β-rhythms simultaneously with the depression of slower and high-amplitude electric fluctuations. Neither was intensification of comparatively rapid and low-amplitude electric components of the electrocorticogram observed during stimulation of a number of elements in the limbic system (tonsils, central gray matter, hypothalamus, etc.), causing the development of defensive emotional reactions.

We also studied the dynamics of the rhythms of various areas of the neocortex during the transition from deep, slow sleep to the desynchronized or paradoxical phase. As is known, the electroencephalographic pattern of the paradoxical phase of sleep is characterized by a depression of slow electric

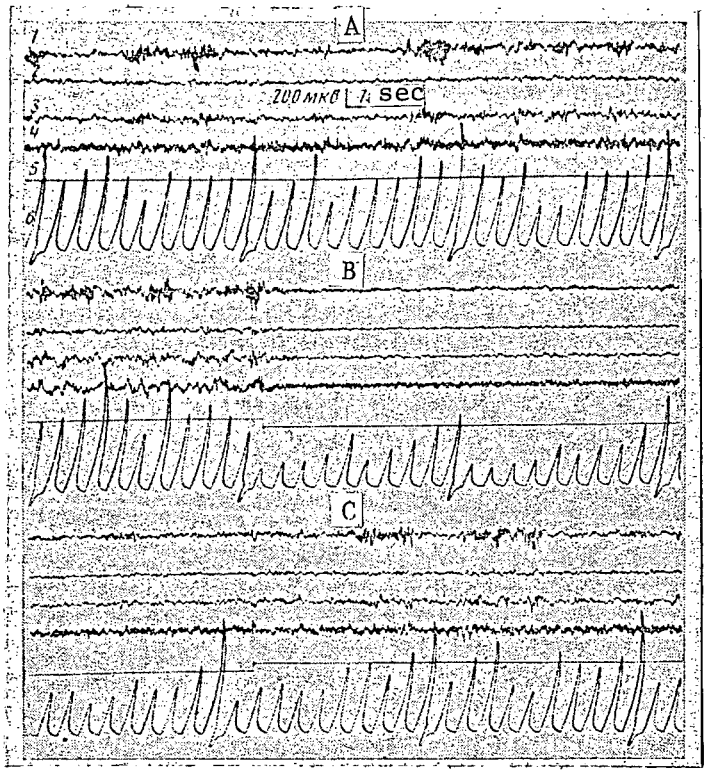

Figure 3. Dynamics of electric activity in the sensory-motor (1), visual (2), associative (3) and auditory (4) regions of the neocortex in a state of drowsiness (A), in response to a conditioned sound stimulus against a background of deep, slow sleep (B) and after the conditioned signal ended (C). 5 - stimulation marking; 6 - integrated rhythm values; δ, θ, α, β_1 and β_2 of the sensory-motor (first five deflections) and the auditory (next five deflections) regions of the neocortex.

activity in the neocortical regions and an increase in comparatively high-frequency and low-amplitude rhythms (Dement and Kleitman [6], Jouvet et al. [10, 11]). This position was also formulated from observations of the dynamics of a total electrocorticogram. Spectral analysis showed, however, that during paradoxical sleep the desynchronization of electric activity in the neocortical

regions is only expressed by a depression of δ, θ and α-rhythms. β_1 and β_2-rhythms do not change significantly.

Results of statistical analysis of a large number of tracings (Figure 4) show that only δ, θ and α-rhythms undergo statistically reliable changes in response to the effect of sound (2) and stimulation of the reticular formation (3). β_1 and β_2-rhythms do not change significantly.

Figure 5 gives the results of a statistical analysis of data obtained from cats which were characterized by pronounced β_1 and β_2-rhythms in the auditory section of the neocortex (A). It is evident that in this case, against a background of desynchronization of the electrocorticogram, the β-rhythms of all neocortical structures, except the auditory region, are not intensified. In the auditory cortex, in response to a conditioned signal (Figure 5, 2), /131 β_2-rhythm increases in comparison with deep, slow sleep (1), but not in comparison with drowsiness (4).

It is clearly evident from the material presented that with desynchronization of slow electric activity of the neocortex, depression only develops in the comparatively slow and high-amplitude electric fluctuations, whereas the comparatively rapid and low-amplitude fluctuations do not undergo significant changes.

In considering the importance of this fact, we proceed from the assumption that the various rhythms of the electroencephalogram are independent of each other in their origin and development (Yokota and Fujimori [14], Rusinov [3], Grindel' et al. [1, 2]). Our data also support this thesis. In particular, β-rhythms of the electroencephalogram of a cat must not be considered as a harmonic of slower or more rapid rhythms, as is asserted by Shminke [4] in relation to the electroencephalogram of man. The fact that the β-rhythm in the electroencephalogram of a cat cannot be a harmonic of slower fluctuations is indicated by the following facts. 1) As is evident from Figure 3, A,

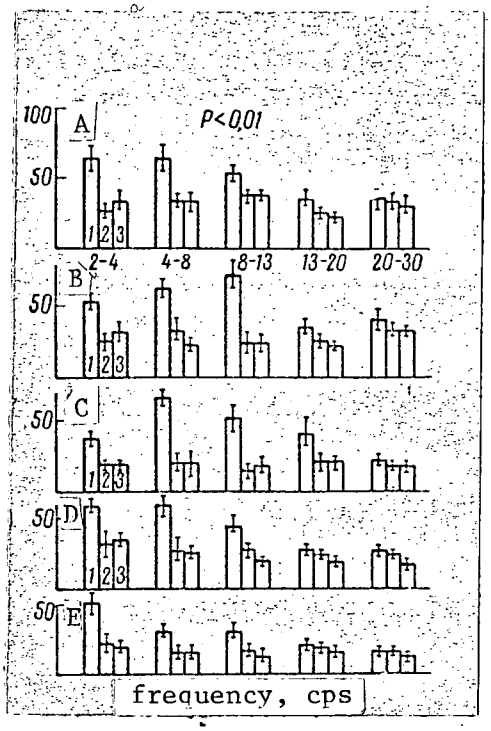

Figure 4. Dynamics of various rhythms of the auditory (A), sensory-motor (B), prefrontal (C), sincipital associative (D) and visual (E) sections of the neocortex in a state of drowsiness (1), in response to a conditioned tone (2) and in response to stimulation of the mesencephalic reticular formation (3).

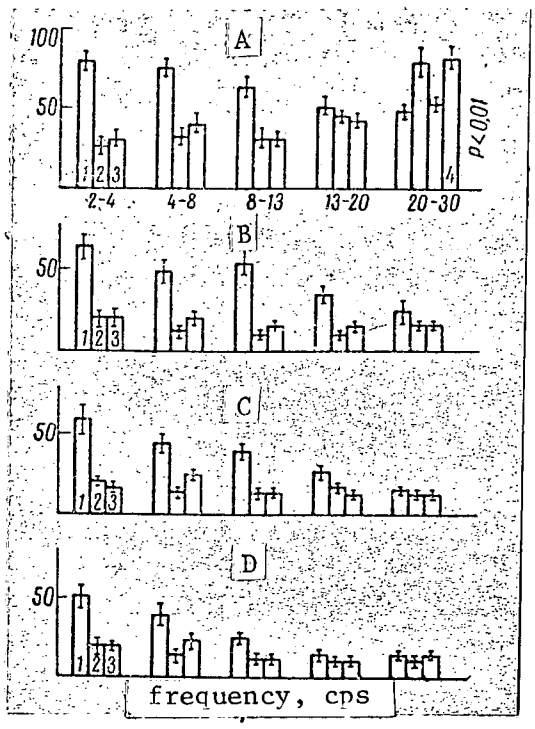

Figure 5. Dynamics of various rhythms of the auditory (A), sensory-motor (B), sincipital associative (C) and visual (D) regions of the neocortex in deep slow sleep (1), in response to a conditioned sound (2), in the paradoxical stage of sleep (3) and during a state of drowsiness (4).

in a state of drowsiness, the β_2-rhythm significantly exceeds δ, θ and α-rhythms in amplitude in the auditory cortex. It is difficult to assume that a second and third harmonic would exceed the first harmonic. 2) From Figure 3, B it is evident that during deep, slow sleep the β_2-rhythm in the auditory cortex is sharply depressed in comparison with a state of drowsiness (Figure 3, A) despite the absence here of a significant change in the α-rhythm. This fact also indicates the independence of the β-rhythm from slower fluctuations. /132 3) If the awakening of the animal occurs against a background of deep slow sleep, when all slow rhythms are depressed, the β_2-rhythm not only is not

depressed, as must be expected in considering it as a harmonic of slower rhythms, but, on the contrary, it gradually increases. Thus, under certain conditions, various rhythms of the electroencephalogram can change in diametric opposition to one another, which indicates their independence. 4) Proceeding from the thesis of Shminke [4], the θ-rhythm can also be considered as a harmonic of slower fluctuations, particularly δ-rhythm. However, this assumption is contradicted by the fact that during stimulation of the reticular formation a sharp increase occurs in the θ-rhythm of the hippocampus simultaneously with a depression of the δ-rhythm (Figure 1, B).

It follows from all that has been said that electroencephalogram rhythms of a higher order (β_1 and β_2) must not be considered as harmonics of slower fluctuations. It is possible that harmonics play a definite role and to some degree distort the pattern, but evidently a spectral analysis basically gives reliable information about the dynamics of electroencephalogram rhythms during various functional states of the brain. If this is the case, the fact described above definitely corrects the traditional thesis that with desynchronization of the electroencephalogram there is an intensification and increase in frequency of rapid fluctuations along with a depression of slow waves. Evidently this inaccuracy was determined by the fact that, in observations of /133
the dynamics of an electroencephalogram, rapid and low-amplitude fluctuations (which mask slower and higher-amplitude fluctuations during sleep) show up better against a background of desynchronization and a false impression is created about their intensification and increase in frequency.

In this respect our conclusion completely agrees with the point of view of V. S. Rusinov [3], expressed back in 1960 in relation to the dynamics of electroencephalogram rhythms of man.

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